Population Models: Part II

Markov Chains and Diffusion Approximations

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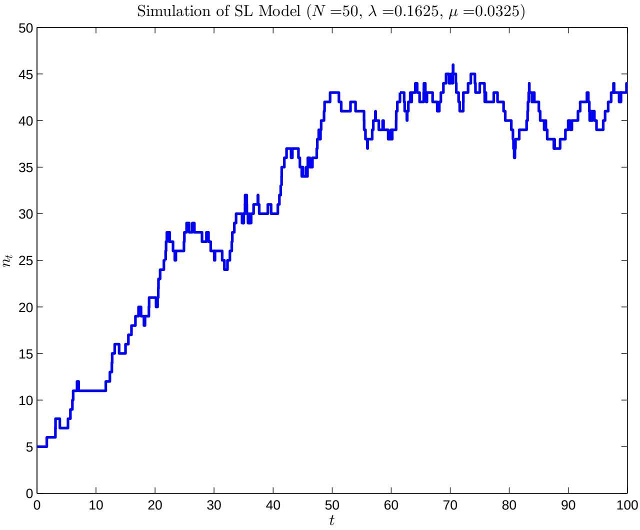
UQ School of Mathematics and Physics

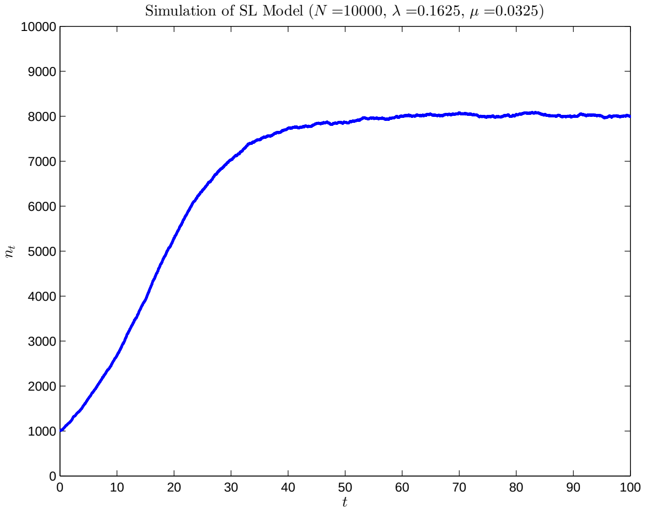
Mathematics Enrichment Seminars

24 August 2016

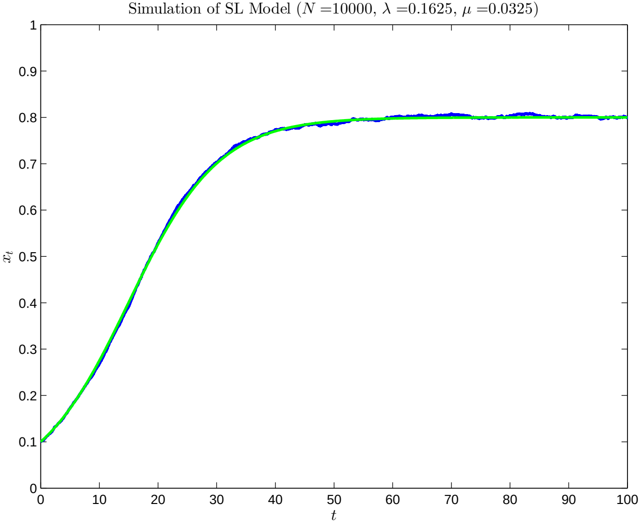
Executive Summary - Simulation of the SL Model ($N = 50$)



Executive Summary - Simulation of the SL Model (N large)



Executive Summary - Solution to deterministic model



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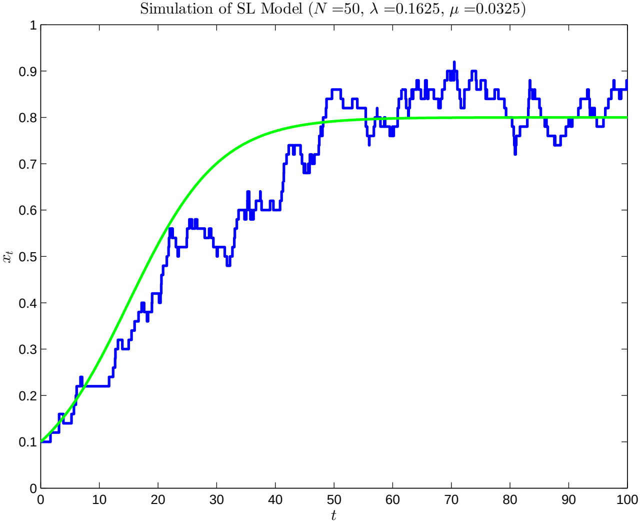
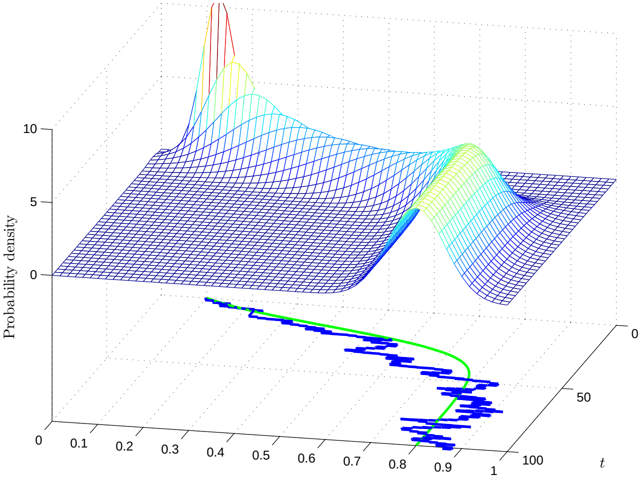
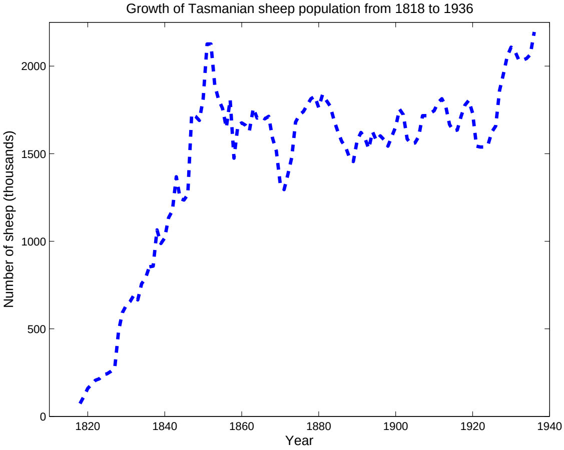


Executive Summary - Normal approximation



Part I Recap: Sheep in Tasmania



Davidson, J. (1938) On the growth of the sheep population in Tasmania. *Trans. Roy. Soc. Sth. Austral.* 62, 342–346.

Part I Recap: The Verhulst-Pearl Model (Logistic Model)

We started with a simple deterministic model for n_t, the number in our population at time t:

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right),$$

with r being the growth rate with unlimited resources and K being the "natural" population size (the *carrying capacity*).

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Integration gives

$$n_t = \frac{K}{1 + \left(\frac{K - n_0}{n_0}\right) e^{-rt}}, \qquad t \geq 0.$$

(As covered in MATH1052 !)

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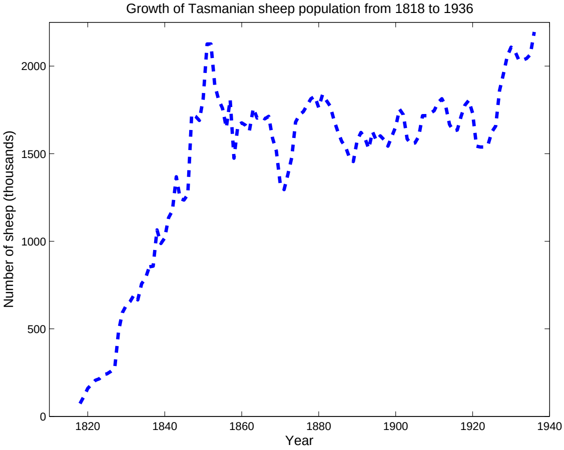

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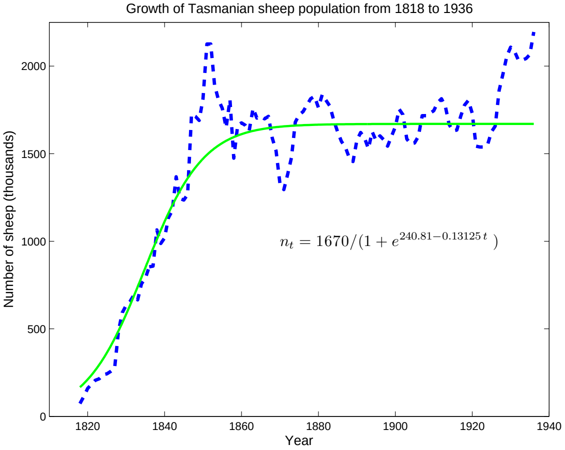

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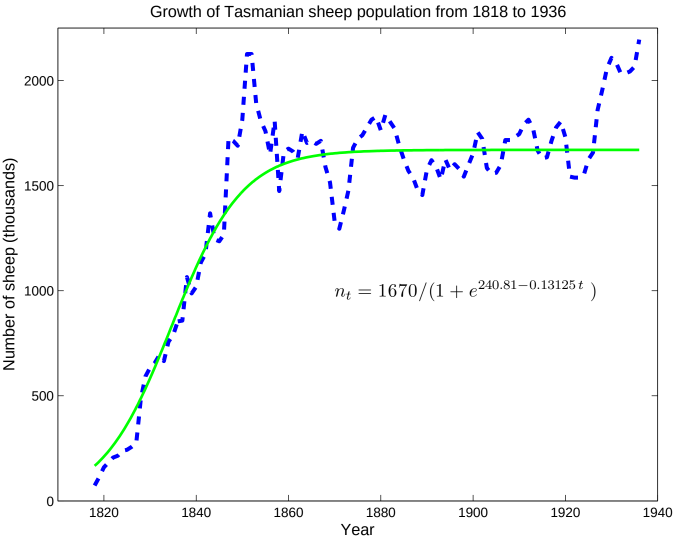
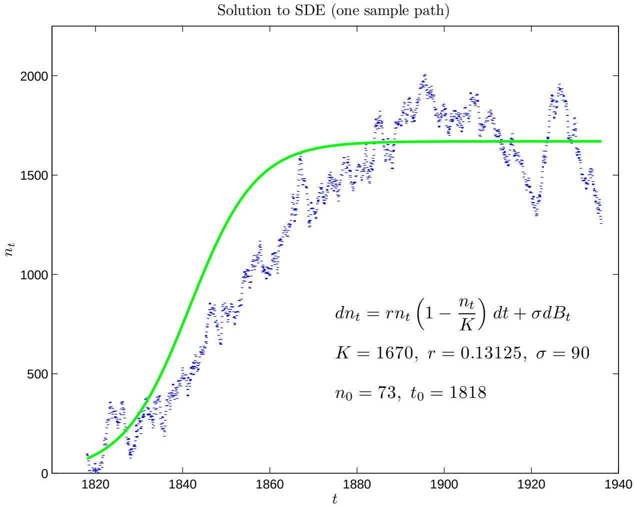
In Matlab ...

```
n = n + r*n*(1-n/K)*h + sigma*sqrt(h)*randn;
```

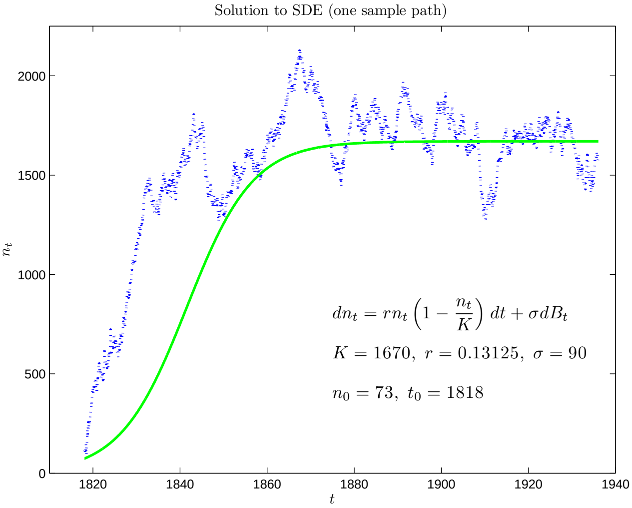

Growth of Tasmanian sheep population from 1818 to 1936
Number of sheep (thousands)
2000
1500
1000
500
0
1820
1840
1860
1880
1900
1920
1940
Year
$n_t = 1670/(1 + e^{240.81 - 0.13125\,t})$

Part I Recap: Solution to SDE (Run 1)



(Solution to the deterministic model is in green)

Part I Recap: Solution to SDE (Run 2)



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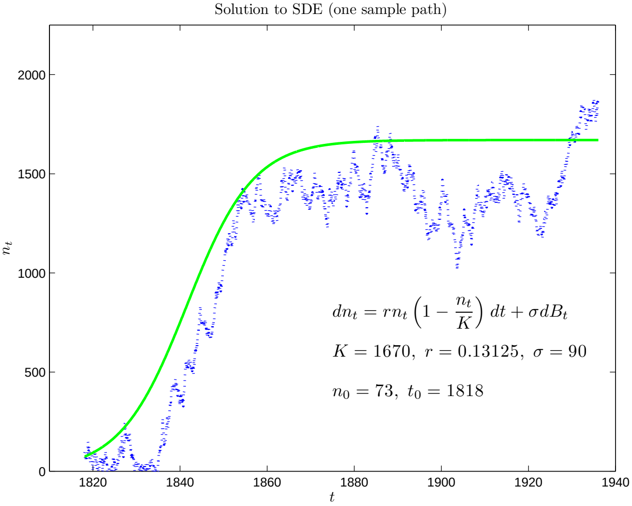
Part I Recap: Solution to SDE (Run 3)



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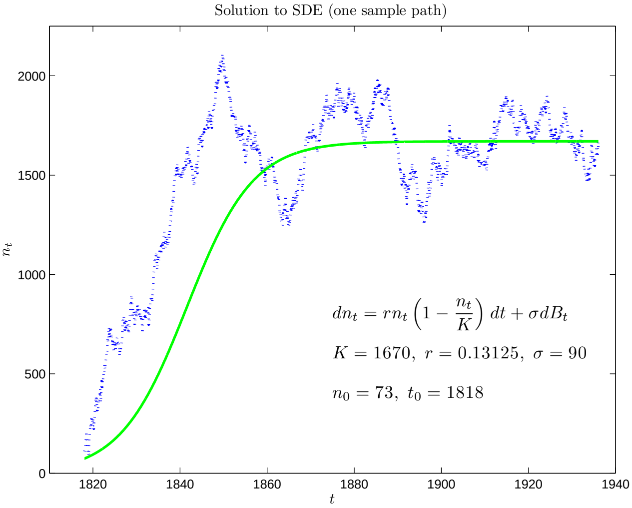

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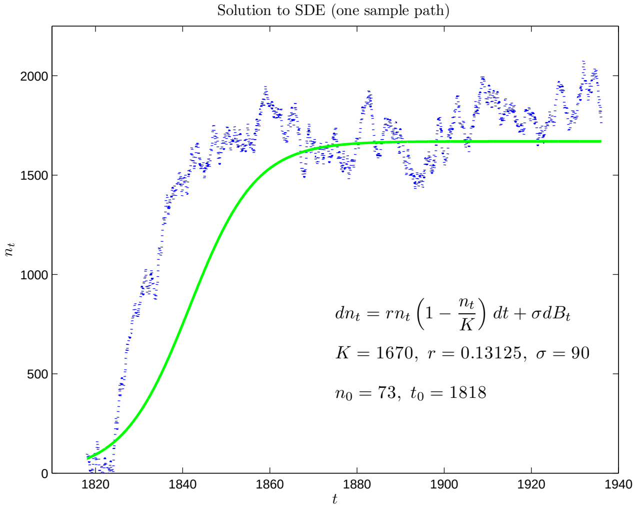
Part I Recap: Solution to SDE (Run 5)



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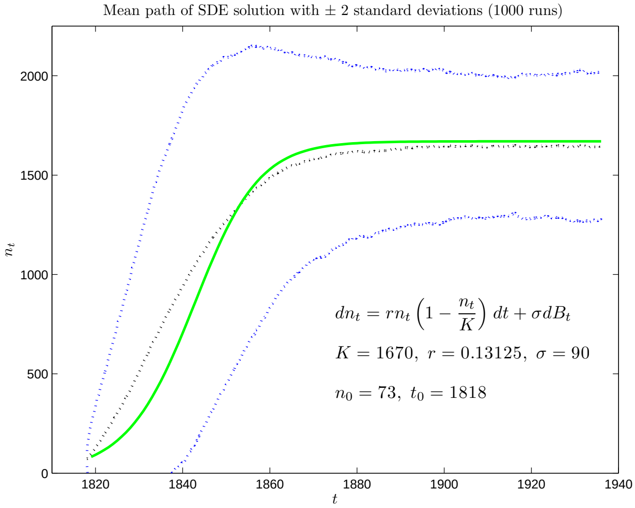
Part I Recap: Solution to SDE



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My last slide from Part I

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Arguably a better approach is to use a continuous-time Markov chain to model n_t.

This will be dealt with in Part II.

A different approach - a continuous time stochastic model

Let's start from scratch specifying a stochastic model with variation being an inherent ingredient: a *Markovian model*.

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We will suppose that n_t evolves (in continuous time) as a birth-death process with transitions

$$\begin{aligned} n &\to n+1 \quad \text{at rate} \quad \frac{\lambda}{N} n(N-n) && \text{(birth)} \\ n &\to n-1 \quad \text{at rate} \quad \mu n && \text{(death)} \end{aligned}$$

where μ (> 0) is the per-capita death rate and λ (> 0) is the birth rate (per-capita when the population is small). N is the *population ceiling*; n_t now takes values in the set $S = \{0, 1, \ldots, N\}$.

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In the context of general population modelling it is called the *Stochastic Logistic Model* (for reasons that will become apparent soon), and can be traced back to William Feller:

Feller, W. (1939) Die grundlagen der volterraschen theorie des kampfes ums dasein in wahrscheinlichkeitsteoretischer behandlung. *Acta Biotheoretica* 5, 11–40.

ACEMS

The Stochastic Logistic Model

In the epidemiological context it is known as the *SIS (Susceptible-Infectious-Susceptible) Model*, and was introduced by Weiss and Dishon to study infections, in a closed population of N individuals, that do not confer any long lasting immunity.

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The transitions have the interpretation

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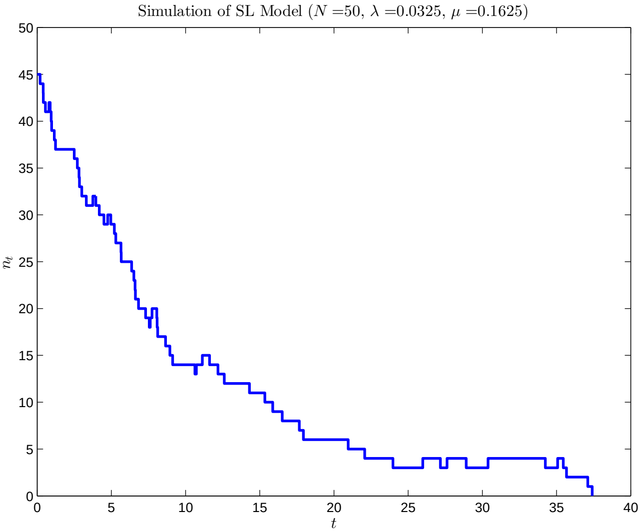
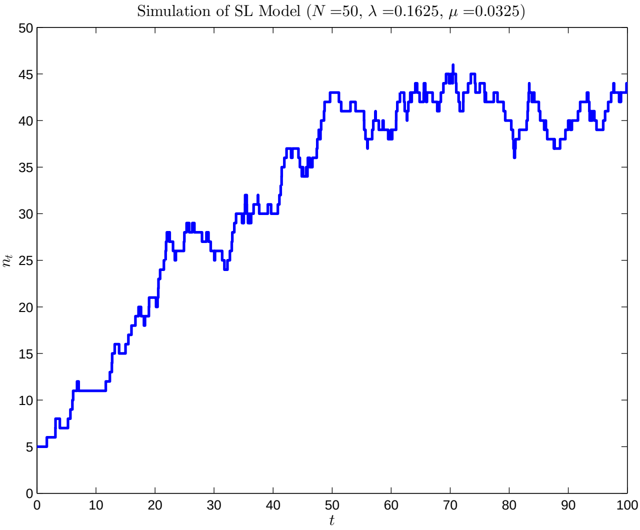
$$n \to n-1 \quad \text{at rate} \quad \mu n \qquad \text{(recovery)}$$

with μ being the per-capita recovery rate and λ being the per-proximate encounter transmission rate.

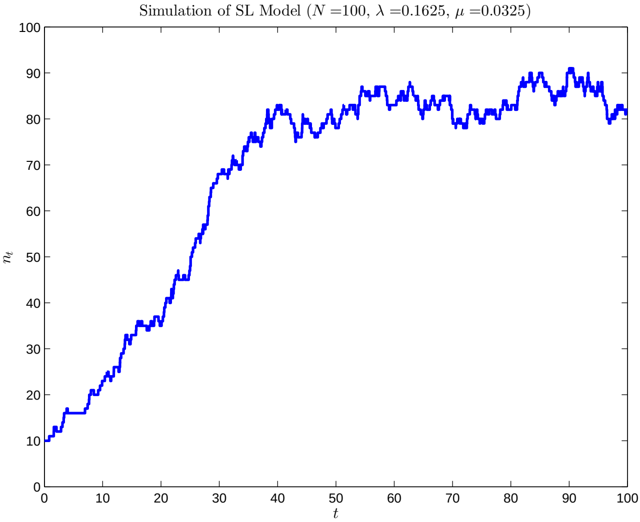
Simulation of the SL Model - extinction



Simulation of the SL Model - persistence



Simulation of the SL Model - N growing



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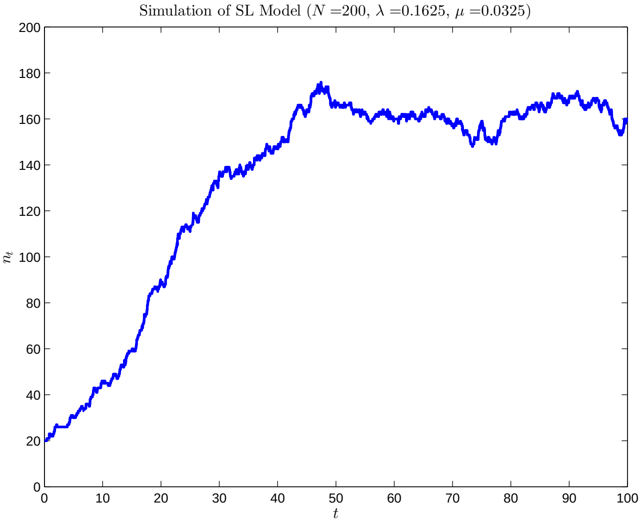

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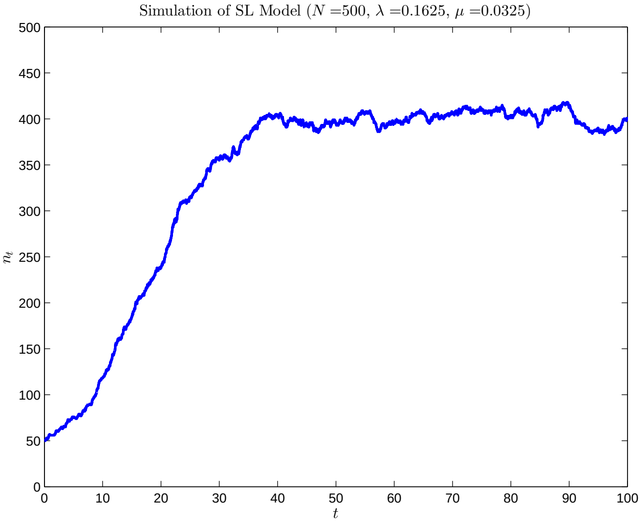

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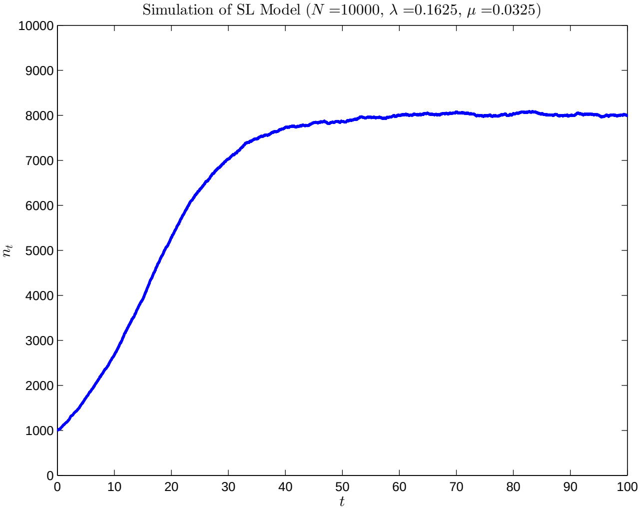

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The key to answering Question 1 is *density dependence*, a property that is shared by the deterministic and stochastic logistic models.

The Verhulst-Pearl Model

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

can be written

$$\frac{1}{N}\frac{dn}{dt} = r\frac{n}{N}\left(1 - \frac{N}{K}\frac{n}{N}\right).$$

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So, letting $x_t = n_t/N$ be the "population density" at time t, we see that

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BTW: How could ODEs possibly be useful for modelling integer-valued quantities such a population size? *Scaling like this helps explain why*.

A stochastic process $(n_t,\ t \geq 0)$ in continuous time taking values in $S \subseteq \mathbb{Z}^k$, called a *Markov chain*, is characterized by its transition rates $Q = (q_{nm},\ n, m \in S)$; q_{nm}, for $m \neq n$, represents the rate at which the process moves form state n to state m.

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Definition (Kurtz*) The model is *density dependent* if there is a subset E of $\mathbb{R}^k$ and a continuous function $f : \mathbb{Z}^k \times E \to \mathbb{R}$, such that

$$q_{n,n+\ell} = N f_\ell \left(\frac{n}{N} \right), \quad \ell \neq 0,\ \ell \in \mathbb{Z}^k.$$

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The mean path of a density dependent Markovian model

Consider the *forward equations* for the *state probabilities* $p_n(t) := \Pr(n_t = n)$ (in statistical mechanics, the *master equation*):

$$p_n'(t) = -q_n p_n(t) + \sum_{m \neq n} p_m(t) q_{mn}, \qquad n \in S,$$

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So, if $q_{n,n+\ell} = N f_\ell(n/N)$ (density dependence), then

$$\frac{d}{dt}\,\mathbb{E}(n_t) = -\sum_n \sum_{\ell \neq 0} N f_\ell(n/N) n p_n(t) + \sum_m p_m(t) \sum_{\ell \neq 0} (m+\ell) N f_\ell(m/N)$$

$$= \sum_m p_m(t) N \sum_{\ell \neq 0} \ell f_\ell(m/N) = N\,\mathbb{E}\left(\sum_{\ell \neq 0} \ell f_\ell(n_t/N)\right).$$

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So, for an arbitrary density dependent Markovian model, we may write

$$\frac{d}{dt}\,\mathbb{E}(n_t) = N\,\mathbb{E}\left(F\left(\frac{n_t}{N}\right)\right),$$

where $F : E \to \mathbb{R}$ is given by

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Warning: I'm not saying that the mean population density satisfies the ODE

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where $F : E \to \mathbb{R}$ is given by

$$F(x) = \sum_{\ell \neq 0} \ell f_\ell\,(x)\,, \qquad x \in \mathbb{R}^k.$$

Or, setting $X_t = n_t/N$ (the "*density process*"),

$$\frac{d}{dt}\,\mathbb{E}(X_t) = \mathbb{E}\,(F(X_t))\,.$$

Warning: I'm not saying that the mean population density satisfies the ODE

$$\frac{d}{dt}\,\mathbb{E}(X_t) = F\,(\mathbb{E}(X_t))\,.$$

But, it's an obvious candidate for our (limiting, we hope) deterministic model for the population density.

The Stochastic Logistic Model is density dependent

For the Stochastic Logistic Model we have $S = \{0, 1, \dots, N\}$ with

$$q_{n,n+1} = \frac{\lambda}{N} n (N - n) = N\lambda \frac{n}{N} \left(1 - \frac{n}{N}\right) \quad \text{and} \quad q_{n,n-1} = \mu n = N\mu \frac{n}{N}.$$

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Therefore, $f_{+1}(x) = \lambda x (1 - x)$ and $f_{-1}(x) = \mu x$, $x \in E := [0, 1]$, and so

$$F(x) = \sum_{\ell \neq 0} \ell f_\ell (x) = f_{+1}(x) - f_{-1}(x) = \lambda x (1 - \rho - x), \qquad x \in E,$$

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where $\rho = \mu/\lambda$. Now compare $F(x)$ with the right-hand side of the Verhulst-Pearl Model for the density process:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{E}\right), \quad \text{where} \quad E = K/N. \tag{1}$$

If $K \sim \beta N$ for N large, so that $K/N \to \beta$, then we may identify β with $1 - \rho$ and r with $\lambda\beta$, and discover that (1) can be rewritten as $dx/dt = F(x)$.

What about convergence?

Recall that $(n_t,\ t \geq 0)$ is a continuous-time Markov chain taking values in $S \subseteq \mathbb{Z}^k$ with transition rates $Q = (q_{nm},\ n, m \in S)$, and we have identified a quantity N, usually related to the size of the system being modelled.

The model is assumed to be *density dependent*: there is a subset E of $\mathbb{R}^k$ and a continuous function $f : \mathbb{Z}^k \times E \to \mathbb{R}$, such that

$$q_{n,n+\ell} = N f_\ell \left(\frac{n}{N} \right), \quad \ell \neq 0,\ \ell \in \mathbb{Z}^k.$$

We set $F(x) = \sum_{\ell \neq 0} \ell f_\ell(x)$, $x \in E$.

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Now formally define the *density process* $(X_t^{(N)})$ by $X_t^{(N)} = n_t/N$, $t \geq 0$. We hope that $(X_t^{(N)})$ becomes more deterministic as N gets large.

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To simplify the statement of results, I'm going to assume that the state space S is finite.

A law of large numbers

The following *functional law of large numbers* establishes convergence of the family $(X_t^{(N)})$ to the unique trajectory of an appropriate approximating deterministic model.

Theorem (Kurtz*) Suppose F is Lipschitz continuous[1]. If $\lim_{N\to\infty} X_0^{(N)} = x_0$, then the density process $(X_s^{(N)})$ converges in probability uniformly on $[0,t]$ to (x_s), the unique (deterministic) trajectory satisfying

$$\frac{d}{ds}x_s = F(x_s), \qquad x_s \in E,\ s \in [0,t].$$

Kurtz, T. (1970) Solutions of ordinary differential equations as limits of pure jump Markov processes, *J. of Appl. Probab.* 7, 49–58.

[1] For some $M > 0$, $|F(x) - F(y)| \leq M|x - y|$ for all $x \in E$.

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(If S is an infinite set, we have the additional conditions $\sup_{x\in E}\sum_{\ell\neq 0}|\ell| f_\ell(x) < \infty$ *and* $\lim_{d\to\infty}\sum_{|\ell|>d}|\ell| f_\ell(x) = 0$, $x \in E$.*)*

[1] For some $M > 0$, $|F(x) - F(y)| \leq M|x - y|$ for all $x \in E$.

A law of large numbers

Convergence in probability uniformly on $[0,t]$ means that, for every $\epsilon > 0$,

$$\lim_{N\to\infty} \Pr\left(\sup_{s\in[0,t]} \left|X_s^{(N)} - x_s\right| > \epsilon\right) = 0.$$

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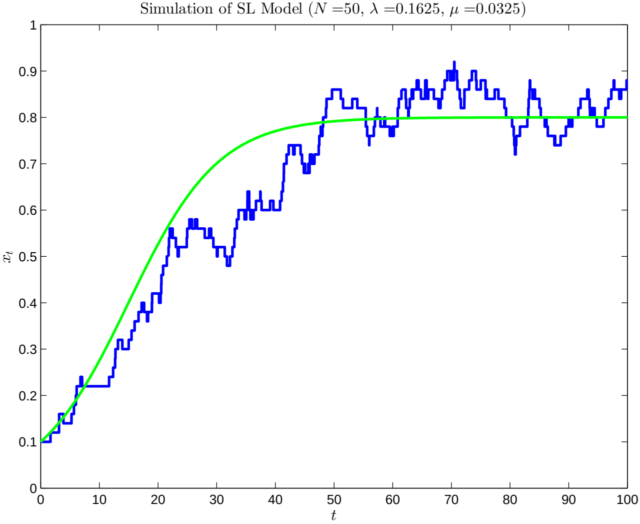
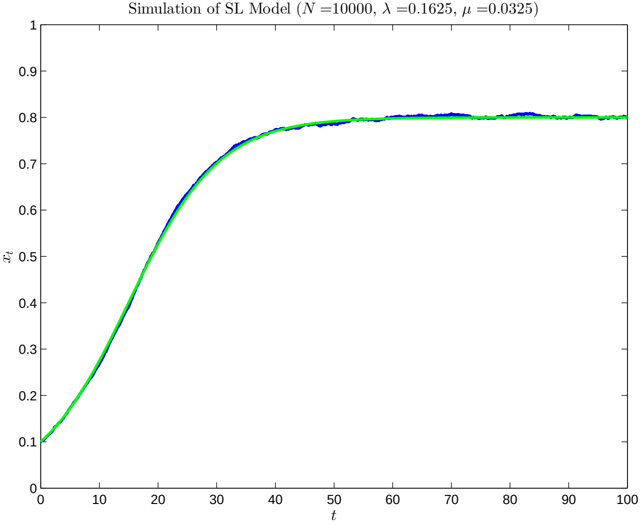
For the Stochastic Logistic Model, it is is easy to check that $F(x) = \lambda x(1-\rho-x)$ is Lipschitz continuous on $E = [0,1]$. So, provided $X_0^{(N)} \to x_0$ as $N \to \infty$, the population density $(X_t^{(N)})$ converges (uniformly in probability on finite time intervals) to the solution (x_t) of the deterministic model

$$\frac{dx}{dt} = \lambda x(1-\rho-x) \qquad (x_t \in E).$$

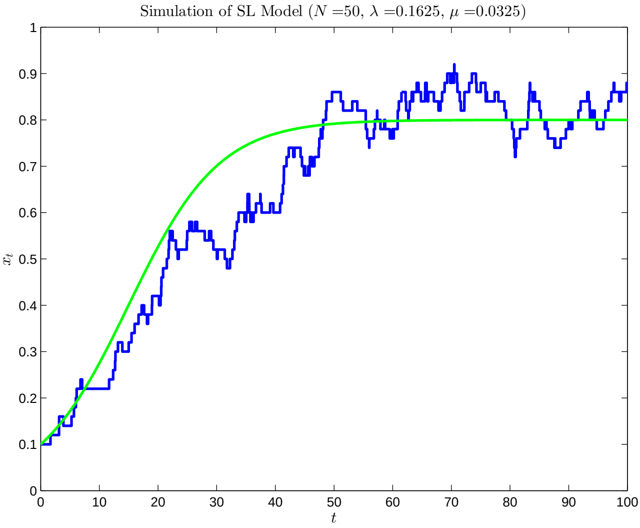
Simulation of the SL Model with x_t ($N = 50$)



Simulation of the SL Model with x_t - N large



Simulation of the SL Model with x_t



Fluctuations about the deterministic trajectory

In a later paper Kurtz* proved a *functional central limit law* which establishes that, for large N, the fluctuations about the deterministic trajectory follow a *Gaussian diffusion*, provided that some mild extra conditions are satisfied.

He considered the family of processes $\{(Z_t^{(N)})\}$, indexed by N, and defined by

$$Z_s^{(N)} = \sqrt{N}\left(X_s^{(N)} - x_s\right), \qquad s \in [0, t].$$

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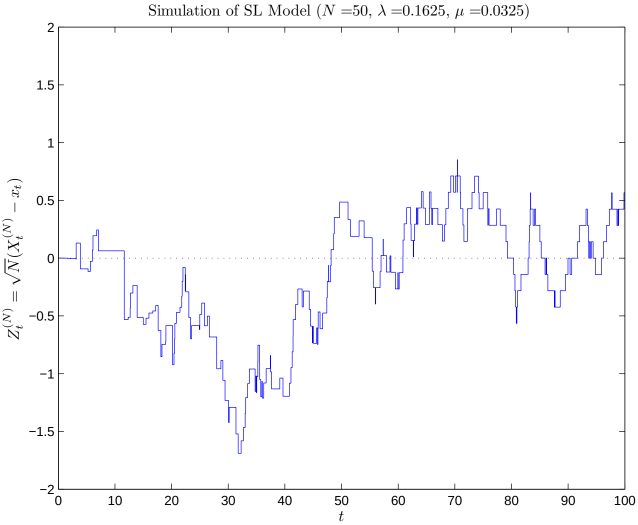
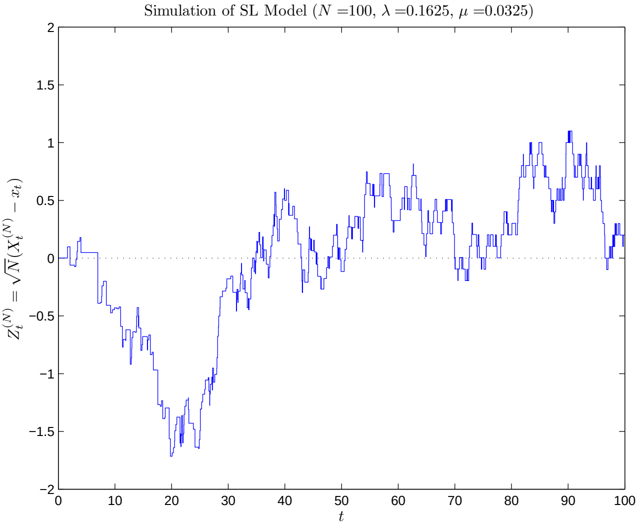
Keep in mind the *Central Limit Theorem*. As applied to coin tossing (de Moivre ($\simeq$1733)), if p_N is the proportion of "Heads" after N tosses of a fair coin,

$$\sqrt{N}\left(p_N - \tfrac{1}{2}\right) \xrightarrow{D} Z \sim N(0, \tfrac{1}{4}), \qquad \text{as } N \to \infty.$$

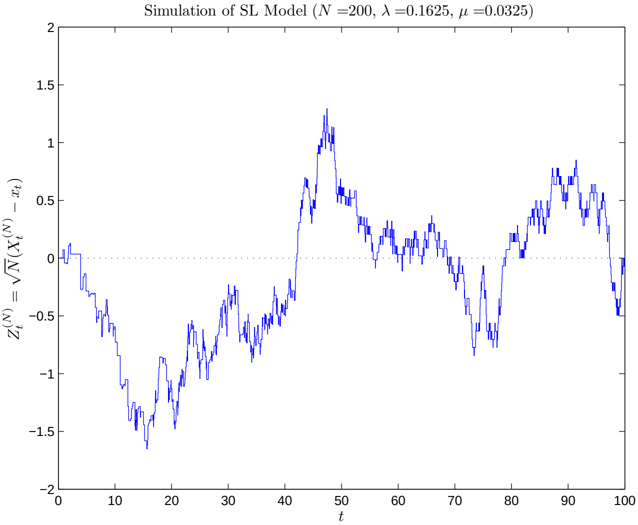
(STAT1201: the normal approximation to the binomial distribution.)


Simulation of SL Model (N =50, λ =0.1625, μ =0.0325)
$Z_t^{(N)} = \sqrt{N}(X_t^{(N)} - x_t)$
t
2
1.5
1
0.5
0
−0.5
−1
−1.5
−2
0
10
20
30
40
50
60
70
80
90
100

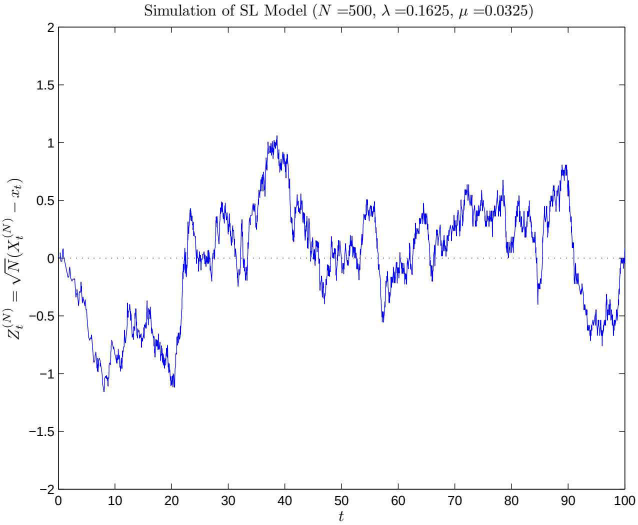
Scaled fluctuations in the SL Model ($N = 100$)



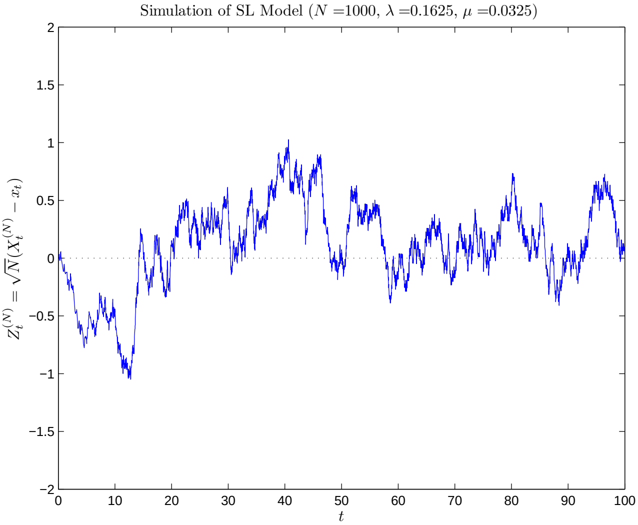
Scaled fluctuations in the SL Model ($N = 200$)



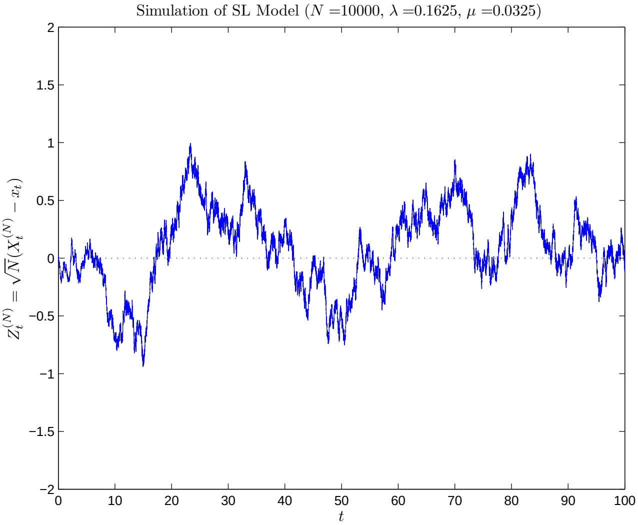
Scaled fluctuations in the SL Model ($N = 500$)



Scaled fluctuations in the SL Model ($N = 1\,000$)



Scaled fluctuations in the SL Model ($N = 10\,000$)



Theorem Suppose that F is Lipschitz continuous and has uniformly continuous first derivatives on E, and that the $k \times k$ matrix $G(x)$, defined for $x \in E$ by $G_{ij}(x) = \sum_{\ell \neq 0} \ell_i \ell_j f_\ell(x)$, is uniformly continuous on E.

Let (x_t) be the unique deterministic trajectory starting at x_0 and suppose that $\lim_{N\to\infty} \sqrt{N}\left(X_0^{(N)} - x_0\right) = z$.

Then, $\{(Z_t^{(N)})\}$ converges weakly in $D[0,t]$ (the space of right-continuous, left-hand limits functions on $[0,t]$) to a Gaussian diffusion (Z_t) with initial value $Z_0 = z$ and with mean given by $\mu_s := \mathbb{E}(Z_s) = M_s z$, where $M_s = \exp(\int_0^s B_u\, du)$ and $B_s = \nabla F(x_s)$, and covariance given by

$$\Sigma_s := \mathrm{Cov}(Z_s) = M_s \left(\int_0^s M_u^{-1} G(x_u) (M_u^{-1})^T \, du \right) M_s^T \, .$$

A central limit law

The functional central limit theorem tells us that, for large N, the scaled density process $Z_t^{(N)}$ can be approximated *over finite time intervals* by the Gaussian diffusion (Z_t).

In particular, for all $t > 0$, $X_t^{(N)}$ has an approximate normal distribution with $\mathrm{Cov}(X_t^{(N)}) \simeq \Sigma_t/N$.

We usually take $X_0^{(N)} = x_0$, for all N, thus giving $\mathbb{E}(X_t^{(N)}) \simeq x_t$.

A central limit law for the SL Model

For the SL Model we have $F(x) = \lambda x(1 - \rho - x)$, and the solution to $dx/dt = F(x)$ is

$$x_t = \frac{(1-\rho)x_0}{x_0 + (1-\rho-x_0)e^{-\lambda(1-\rho)t}}.$$

Then, $\mathbb{E}(X_t^{(N)}) \simeq x_t$.

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Then, $\mathbb{E}(X_t^{(N)}) \simeq x_t$. We also have $F'(x) = \lambda(1-\rho-2x)$ and

$$G(x) = \sum_\ell \ell^2 f_\ell(x) = \lambda x(1+\rho-x) = F(x) + 2\mu x,$$

giving

$$M_t = \exp\left(\int_0^t F'(x_s)\,ds\right) = \frac{(1-\rho)^2 e^{-\lambda(1-\rho)t}}{(x_0+(1-\rho-x_0)e^{-\lambda(1-\rho)t})^2}.$$

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We can evaluate $v_t := \mathrm{Var}(Z_t) = M_t^2 \left(\int_0^t G(x_s)/M_s^2\, ds\right)$ numerically.

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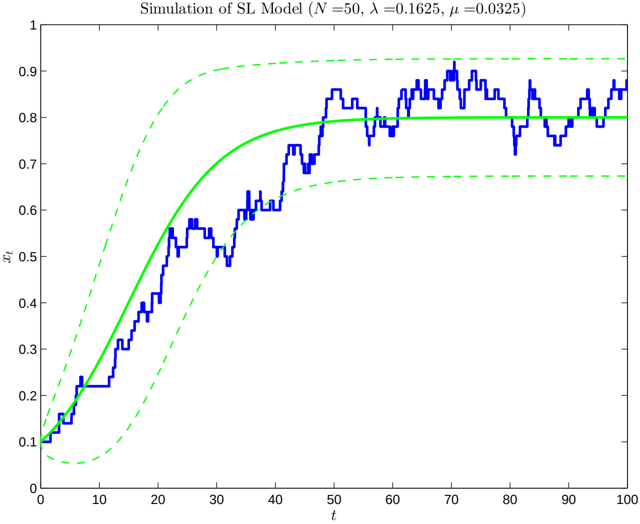
$$v_t = x_0\Big(\rho x_0^3 + x_0^2(1+5\rho)(1-\rho-x_0)e^{-\lambda(1-\rho)t} + 2x_0(1+2\rho)(1-\rho-x_0)^2(\lambda(1-\rho)t)e^{-2\lambda(1-\rho)t}$$
$$-\left((1-\rho-x_0)[3\rho x_0^2+(2+\rho)(1-\rho)x_0-((1+2\rho))(1-\rho)^2]+\rho(1-\rho)^3\right)e^{-2\lambda(1-\rho)t}$$
$$-(1+\rho)(1-\rho-x_0)^3 e^{-3\lambda(1-\rho)t}\Big)\Big/\Big(x_0+(1-\rho-x_0)e^{-\lambda(1-\rho)t}\Big)^4.$$

Then, $\mathrm{Var}(X_t^{(N)}) \simeq v_t/N$.

Simulation of the SL Model with $x_t \pm 2\sqrt{v_t/N}$



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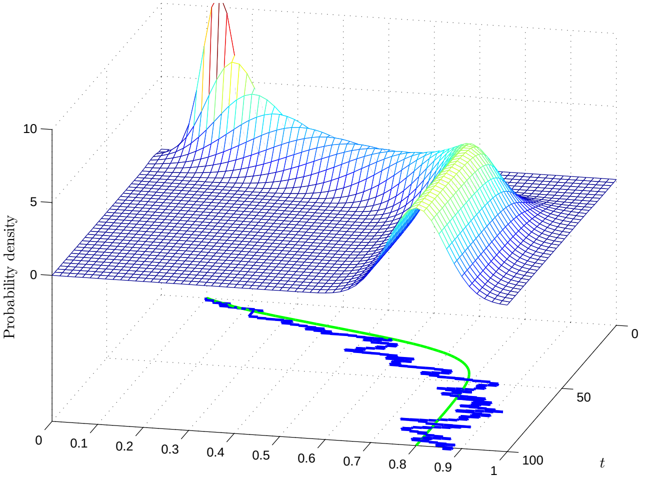
Simulation of the SL Model with Normal approximation



The OU approximation

If the initial point x_0 of the deterministic trajectory is chosen to be an equilibrium point of the deterministic model, we can be far more precise about the approximating diffusion.

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Corollary If x_{eq} satisfies $F(x_{\mathrm{eq}}) = 0$, then, under the conditions of the theorem, the family $\{(Z_t^{(N)})\}$, defined by

$$Z_s^{(N)} = \sqrt{N}(X_s^{(N)} - x_{\mathrm{eq}}), \qquad 0 \le s \le t, \qquad s \in [0, t].$$

converges weakly in $D[0, t]$ to an *Ornstein–Uhlenbeck (OU) process* (Z_t) with initial value $Z_0 = z$, local drift matrix $B = \nabla F(x_{\mathrm{eq}})$ and local covariance matrix $G(x_{\mathrm{eq}})$.

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In particular, Z_s is normally distributed with mean and covariance given by $\mu_s := \mathbb{E}(Z_s) = e^{Bs}z$ and

$$\Sigma_s := \mathrm{Cov}(Z_s) = \int_0^s e^{Bu} G(x_{\mathrm{eq}}) e^{B^T u}\, du\,.$$

The OU approximation

Note that

$$\Sigma_s = \int_0^s e^{Bu} G(x_{\mathrm{eq}}) e^{B^T u}\, du = V_\infty - e^{Bs} V_\infty e^{B^T s},$$

where V_∞, the stationary covariance matrix, satisfies

$$B V_\infty + V_\infty B^T + G(x_{\mathrm{eq}}) = 0.$$

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Finally, this brings us "full circle" to the approximating SDE

$$dn_t = -\alpha(n_t - K)\, dt + \sqrt{2N\alpha\rho}\, dB_t,$$

where $\alpha = \lambda(1-\rho)$.

Simulation of the SL Model with $x_{\text{eq}} \pm 2\sqrt{v_t/N}$ (OU Approximation)